

AN EARLY MIOCENE PINNIPED OF THE GENUS *DESMATOPHOCA* (MAMMALIA: OTARIIDAE) FROM WASHINGTON

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ABSTRACT. The extinct otariid pinniped genus *Desmatophoca* Condon, 1906, is represented by two rare sea lion-like species that are relatively large and highly derived, in comparison with most other contemporaneous fossil otariids. The type and only previously described species of the genus is *Desmatophoca oregonensis* Condon, 1906, which was known only by the holotype skull and a questionably referred humerus from late Early to early Middle Miocene rocks referred to the Astoria Formation in Oregon, U.S.A. Another partial skull from the same formation is referred here to the same species.

A new species of *Desmatophoca*, *D. brachycephala*, has been discovered in slightly older rocks of Early Miocene age, also referred to the Astoria Formation, that are exposed on the north side of the Columbia River in Washington, U.S.A. *Desmatophoca brachycephala*, like *D. oregonensis*, is known by a skull of a male. It is distinguished from the latter species by having a relatively wider skull with a shorter rostrum, larger diameter canines, more derived cheek tooth structures, wider interorbital region, and larger mastoid processes. These and other differences make *D. brachycephala* a more derived species than *D. oregonensis*, and indicate that the distinctive otariid subfamily Desmatophocinae existed earlier in time than has previously been documented and must have had a significant early evolutionary history. The group is only known by fossils from the eastern North Pacific margin. Contrary to some previously published statements, there are enough substantial morphological differences between the Desmatophocinae and another fossil subfamily, the Allodesminae, to continue to classify them separately.

INTRODUCTION

Desmatophoca oregonensis Condon, 1906, was one of the first fossil otariid pinnipeds described in the scientific literature, and was for many years also the geologically most ancient one known. This sea lion-like animal has been discussed by many subsequent writers, and has figured in discussions of the origin of the family Otariidae (sensu lato; including sea lions, fur seals, walruses, and fossil taxa), yet it is still relatively poorly understood. It appears to be a rare species and is known in the previously published literature only by the holotype cranium (associated with an undescribed mandible fragment and some incomplete postcranial bones; see Packard and Kellogg, 1934:20) and a subsequently

referred isolated humerus (Packard, 1947). These fossils are all from rocks in the Newport Embayment that have been referred to the Astoria Formation (late Early to early Middle Miocene age), and are exposed on the coast of Oregon near Newport, Lincoln County (Howe, 1926; Packard and Kellogg, 1934:5–19, fig. 1; Moore, 1964; Ray, 1976). I consider the identity of the humerus to be tenuous, and shall not make further reference to it in this study.

Desmatophoca oregonensis has been the subject of widely differing taxonomic opinions. Condon (1906) believed that it had features of the family Otariidae as well as of the Phocidae (true seals). Wortman (1906) made the same claim. He correctly interpreted the species as the most primitive fossil pinniped then known, but gave its age as probably Oligocene and, citing characters he interpreted as similar to those of *Patriofelis* Leidy, 1870, reiterated his earlier (1894) theory that the pinnipeds evolved directly from oxyaenid creodonts. Kellogg (1922), while incorrectly concluding that *D. oregonensis* was younger geologically than another early species, *Allodesmus kernensis* Kellogg, 1922, stated unequivocally (1922:62) that it was a true otariid and not related to phocids. Packard and Kellogg (1934:24) later concluded that *D. oregonensis* was geochronologically older than *A. kernensis*, a currently held view (Barnes, 1972). Mitchell (1966) suggested that *D. oregonensis* was in some ways a suitable ancestor of later true sea lions, or (1968:1888, fig. 16) of all the Otariidae (sensu lato), but later, after the discovery of enaliarctines, he considered it to be an early and aberrant offshoot of the otariid lineage (Mitchell, 1975; and see Barnes, 1972:62). Hay (1930), indicating a more distant relationship, named a new family, the Desmatophocidae, to contain it. Simpson (1945) suggested that Hay's family might instead best be regarded as a subfamily of the Otariidae, but he did not use such a rank in his classification. Mitchell (1966) and Barnes

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(1972) both used the subfamily rank, but they included within the subfamily Desmatophocinae the even more aberrant and highly derived species of *Allodesmus* Kellogg, 1922. Repenning and Tedford (1977:74; see also Repenning, 1976; King, 1983:129–130) recognized a separate family Desmatophocidae within the superfamily Otarioidea, but they retained *Allodesmus* within it. Mitchell (1968, 1975) and Barnes (1979, and in press) classified Desmatophocinae and Alledesminae as equal units, along with several other subfamilies (both extant and extinct), within a single, broadly defined pinniped carnivore family, the Otariidae (see Barnes, Domning, and Ray, 1985:table 1). It is in the latter taxonomic context that I treat the subfamily Desmatophocinae in the present study. The Recent sea lions, fur seals, and walruses were also classified by Hall (1981) within one family, the Otariidae, but he used the subfamily name Rosmarinae rather than Odobeninae for the walruses, and included phocids and otariids in the order Pinnipedia instead of the Carnivora.

Most of the various other fossil species, both named and unnamed, that have been classified in the Desmatophocinae by Mitchell (1966) and Barnes (1972), have subsequently been reassigned to other subfamilies (Mitchell, 1975; Repenning and Tedford, 1977; Barnes, 1979, and in press). The concept and content of the Desmatophocinae has thus become much reduced to include only one named species, *Desmatophoca oregonensis*.

A new fossil species belonging to the genus *Desmatophoca* Condon, 1906, has recently been discovered in Washington, and it is the purpose of this paper to describe and diagnose it. The new specimen is from the Astoria Formation, which is part of a sequence of rocks on the north side of the Columbia River that has been prospected extensively by J.L. Goedert and G.H. Goedert. The type locality of the new species of *Desmatophoca* has produced a diverse assemblage of vertebrates, including other mammals and fishes. Among these are at least two additional species of otariid pinnipeds, but they are not yet known by enough material to be more precisely identified. The invertebrates from the Lincoln Creek Formation, which directly underlies the Astoria Formation near Knappton, have been recently described by Zullo (1982—barnacles), Rigby and Jenkins (1983—sponges), and Moore (1984—mollusks). The latter author reviewed the history of collecting and research in the Knappton area and described the geographic and geologic setting (Moore, 1984:figs. 1, 2).

METHODS AND MATERIALS

The holotype of *Desmatophoca brachycephala*, new species, was originally discovered in at least three separate sections of a broken concretion, and some of its parts are still missing. The different sections were joined with plastic resin, and the same material was also used to fill some vacuities. At the rostral extremity, remnants of the canines and incisors were only tenuously attached by rock matrix to the rest of the cranium. They now retain their original positions relative to the mostly missing extremity of the snout only because of this resin, which was poured in prior to removal of the surrounding rock. For economy and to avoid jeopardizing the

integrity of the specimen, the rock was left within the right orbit. Because of the crushing of the bullae and the hardness of the matrix, it was decided not to attempt to open either tympanic cavity of the holotype at this time.

In the restorations of the skulls (Figs. 3, 4b, 5, 7, 9), only those parts that are preserved on at least one side of a skull are shown in solid lines. All other missing parts are represented by dashed lines. The anatomical terminology used here is adapted from that used by Howell (1928), Miller, Christensen, and Evans (1964), Mitchell (1966, 1968), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). Those skull measurements in Table 1 which are the same as those that were defined by Sivertsen (1954:18–20) are identified by the same numbers, in brackets, that were given them by Sivertsen. Other measurements are as defined by Barnes (1972:fig. 1; 1979:4–5).

A complete synonymy and an emended diagnosis of the subfamily Desmatophocinae are given here. The latter is partly based on characters listed by Mitchell (1968:1893–1894) and by Repenning and Tedford (1977:10–11, 74), with appropriate modifications. Geochronologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979) following the revised radiometric scale of Dalrymple (1979), and the correlations proposed by Addicott (1976), Ray (1976), Armen-trout (1981), and Moore and Addicott (1987).

The acronym, LACM, is for the Natural History Museum of Los Angeles County, Los Angeles, California. An author and date in parentheses following a taxonomic name indicates my use of that name at a different rank than originally proposed. Millions of years ago (mega-annum) is abbreviated ma. Anatomical abbreviations used in the illustrations are explained as follows:

ac—alisphenoid canal
at—auditory tube (= musculotubular canal, including eustachian tube)
Bo—basioccipital
Bs—basisphenoid
cc—carotid canal (posterior aperture)
eam—external acoustic meatus
fh—hypoglossal foramen
fi—incisive foramen (= palatine fissure)
fio—infraorbital foramen
fla—anterior lacerate foramen (joined with foramen rotundum as an orbital fissure)
flp—posterior lacerate foramen
fo—foramen ovale
fop—optic foramen
fpal—palatine foramen
fpp—posterior aperture of palatine foramina
Fr—frontal
fsm—stylomastoid foramen
gf—glenoid fossa
hf—tympanohyal pit (= hyoid fossa)
Ju—jugal
mp—mastoid process
Mx—maxilla

Na—nasal
Oc—occipital
occ—occipital condyle
Pa—parietal
Pal—palatine
Pmx—premaxilla
Ps—presphenoid
Pt—pterygoid
pp—paroccipital (= jugular) process
Sq—squamosal
tb—tympanic bulla

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Infraorder Arctoidea Flower, 1869

Parvorder Ursida Tedford, 1976

Family Otariidae Gill, 1866

INCLUDED SUBFAMILIES. Enaliarctinae Mitchell and Tedford, 1973; Otariinae (Gill, 1866); Desmatophocinae (Hay, 1930); Allodesminae (Kellogg, 1931); Imagotariinae Mitchell, 1968; Dusignathinae Mitchell, 1968; Odobeninae (Allen, 1880).

Subfamily Desmatophocinae (Hay, 1930)
Mitchell, 1966

Desmatophocidae Hay, 1930:557, as a family of the suborder Pinnipedia, order Carnivora, to include *Desmatophoca*.
Desmatophocinae (part). Mitchell, 1966:4, 39, 40; Barnes, 1972:5, as a subfamily of the family Otariidae, to include *Desmatophoca*, *Allodesmus*, and less precisely identified species, and, according to Mitchell (1966:39, 40), *Dusignathus* Kellogg, 1927, as well.
Desmatophocinae (Hay, 1930). Mitchell, 1968:1839; Barnes, 1979:38, as a subfamily of Otariidae, exclusive of Allodesminae.
Desmatophocidae (part). Repenning and Tedford, 1977:10, 74–76, as a family of the superfamily Otarioidea, to include *Desmatophoca*, *Allodesmus*, and less precisely identified species.

EMENDED DIAGNOSIS OF SUBFAMILY. A subfamily of the family Otariidae differing from Enaliarctinae by having crania without an embayment in the lateral edge of the basioccipital for a loop of the median branch of the internal carotid artery and by lacking carnassial teeth; differing from all other subfamilies except Allodesminae by having tympanic crest not projecting into tympanic cavity, and by having nasal bones elongate and tapering posteriorly and inserted between frontals (character not yet determined for Imagotariinae and Dusignathinae); differing from Otariinae, Dusignathinae, Imagotariinae, and Odobeninae by having large, elongate posterolaterally directed paroccipital

Table 1. Measurements of holotype skull, LACM 120199, of *Desmatophoca brachycephala*, new species, in mm. Parentheses indicate estimated measurements. Brackets indicate measurements explained by Sivertsen (1954:18–20), and the method of taking the other measurements follows Barnes (1972, 1979, in press).

Total length	(283)
Anterior border of orbit to tip of snout	(80)
External acoustic meatus to anterior border of orbit	135.0
Anterior border of orbit to tip of nasals	(28)
Post-palatal length (palatal notch to basion)	121.3
Basion to anterior edge of zygomatic root [18]	188.0
Length of tooth row, C to M ¹	(88)
Length of tooth row, P ¹ –M ¹	62.5
Width of rostrum across canines [12]	(80)
Width of palate across base of P ³ alveoli	(34)
Width of palate across alveoli of P ²	(64)
Width of palate across anterior alveoli of P ⁴	(80)
Width between infraorbital foramina	65.0
Width across greatest interorbital constriction [6]	40.0
Width across supraorbital processes [7]	37.5
Width across greatest intertemporal constriction	(30.0)
Width of braincase at anterior edge of glenoid fossa [8]	(73)
Zygomatic width [17]	184.0
Auditory width [19]	142.0
Mastoid width [20]	168.0
Paroccipital width	(126)
Greatest width across occipital condyles	69.8
Greatest width of anterior nares	(35)
Greatest height of anterior nares	(31)
Width of zygomatic root of maxilla [14]	22.0
Greatest width of foramen magnum	32.1
Greatest height of foramen magnum	22.5
Least depth of jugal	12.0
Transverse diameter of infraorbital foramen	15.0
Anteroposterior diameter left C alveolus	(26.5)
Anteroposterior diameter right P ¹ alveolus	(12.8)
Anteroposterior diameter right P ⁴ alveoli	12.2
Anteroposterior diameter right M ¹ alveolus	7.2

process which is separate from mastoid process and not joined by a crest; differing from most Enaliarctinae, all Otariinae, Imagotariinae, and Odobeninae by having pterygoid process of maxilla enlarged so palate expands ventral to orbit (character not determinable for Dusignathinae); differing from Allodesminae and Odobeninae by having vertical posterior and medial crista on canine crowns; differing from Imagotariinae and Odobeninae by having hyoid fossa separated from stylomastoid foramen by only a thin bridge of bone, not joined by an elongate, narrow sulcus; differing from Otariinae by having posterior lacerate foramen not greatly elongate anteroposteriorly; differing from Allodesminae by having more inflated tympanic bulla, posterior lacerate foramen not expanded transversely, smaller orbit with anterior margin

flared anterodorsally instead of being retracted posteriorly, unreduced incisive foramina, and squamosal-jugal contact not greatly expanded dorsoventrally; and differing further from Odobeninae by having canines which are not modified as tusks.

TYPE AND ONLY INCLUDED GENUS. *Desmatophoca* Condon, 1906.

Desmatophoca Condon, 1906

Desmatophoca Condon, 1906:3.

EMENDED DIAGNOSIS OF GENUS. Identical with that for the subfamily as given above until additional genera are described.

TYPE SPECIES. *Desmatophoca oregonensis* Condon, 1906; type by original monotypy.

INCLUDED SPECIES. *Desmatophoca oregonensis* Condon, 1906, late Early Miocene and/or early Middle Miocene, Oregon; and *Desmatophoca brachycephala*, new species, Early Miocene, Washington.

Desmatophoca oregonensis Condon, 1906

Figures 1, 9a

Desmatophoca oregonensis Condon, 1906:3, 11, figs. 1–3 on p. 9, unnumbered figures on pp. 3, 10.

HOLOTYPE. University of Oregon (Eugene), Museum of Natural History (UOMNH) F735, cranium, partial dentary, and postcranial bones.

TYPE LOCALITY. UOMNH locality 1153, coast near Astoria, Lincoln County, Oregon. The precise collecting locality of the holotype is not known, except that it apparently was west of Newport in the sea cliff where the Astoria formation is exposed (Packard and Kellogg, 1934:20, fig. 1).

REFERRED SPECIMEN. LACM 123285, the anterior part of a cranium with right canine, P²⁻³, and left I³, canine, and P¹⁻³; collected by D.J. Martel, 18 April 1983.

LOCALITY OF REFERRED SPECIMEN. LACM 4851, among boulders on beach midway between the mouths of Schooner and Moloch creeks, approximately 6.5 km north of Newport, Lincoln County, Oregon, as shown on Yaquina, Oregon, United States Geological Survey topographic map, 1:62,500 scale, 1957 edition. Approximately 44°41'45" north latitude and 124°03'55" west longitude. This locality is approximately 0.75 km north of Schooner Point, which was the collecting locality of a referred specimen of the fossil mysticete, *Cophocetus oregonensis* Packard and Kellogg, 1934 (see Packard and Kellogg, 1934:21, fig. 1, item 6).

FORMATION AND AGE. Astoria Formation, late Early Miocene and/or early Middle Miocene. The rocks that have been referred to the Astoria Formation which crop out on the Oregon coast in Lincoln County, near Newport (Packard and Kellogg, 1934:20, fig. 1; Ray, 1976:fig. 2), produced the mollusks that were used to characterize the Newportian Stage (Addicott, 1976:102, 104, fig. 4). The holotype of *D. oregonensis* was found at an unspecified horizon within the Astoria Formation, and the referred rostrum (LACM 123285)

was found at a location near the sea cliff outcrop of the "Iron Mountain bed," a distinctive horizon within the Astoria Formation which produced the dome-skulled chalicothere fossil that was described by Munthe and Coombs (1979). The land mammals and other lines of evidence derived from this same coastal Oregon part of the Astoria Formation provide a correlation with the Hemingfordian or the early part of the Barstovian North American land mammal ages (Ray, 1976:fig. 2; Munthe and Coombs, 1979:78–80). The concordance between these mammal ages and the Newportian Stage represents an interval of time spanning from approximately 19 ma to 15 ma and from the late part of the Early Miocene through the early part of the Middle Miocene (Armentrout, 1981). This then is also the best current estimate of the geologic age of *Desmatophoca oregonensis*.

DISCUSSION. Condon's (1906) original publication (see also Condon, 1910) on *Desmatophoca oregonensis* includes a brief description, photographs of the dorsal and right lateral surfaces of the partially prepared holotype cranium, and drawings of the P⁴. These have been greatly supplemented by additional observations by Wortman (1906), Downs (1956:124–125), Mitchell (1966:36–37; 1968:1883, 1893–1894, table V; 1975:12–14), Barnes (1972:63; 1979:35), and Repenning and Tedford (1977:74). E. Mitchell is supervising further preparation of the holotype. He intends to publish a detailed reassessment of the species (Mitchell, 1975:12), and has already presented illustrations that show the major cranial characters of the holotype (Mitchell, 1966:pl. 29; 1975:fig. 2). The U.S. National Museum of Natural History has provided casts of the holotype of *D. oregonensis*.

The recently collected referred specimen of *Desmatophoca oregonensis* (Fig. 1) closely matches the size and morphology of the holotype, and yields additional information on the structure of the P¹, the P³, and of the posterior part of the palate. Both of the presently available specimens appear to represent male individuals because of the relative sizes of their canines and the development of bony rugosities and tubercles. All of the sutures between the bones of the referred snout remain unfused, but the individual had attained the same size as the holotype specimen at the time of its death. Therefore, the referred specimen must represent a young adult individual. This new specimen helps to confirm as diagnostic for the taxon certain characters of the holotype as: rostrum parallel-sided; cranium high between orbits and sloping anteriorly toward nasal bones; nasals elongate and slightly depressed medially, with closely appressed and tapering posterior ends extending posteriorly to a point dorsal to the middle of the orbit; narial opening sloping gently and narrower ventrally than at the dorsal part; presence of a slight fossa on the anterior surface of the rostrum on the maxilla-premaxilla suture dorsal to the diastem between the I³ and the canine; zygomatic portion of the jugal short and thick, mortised by relatively elongate splints of bone dorsolaterally and ventromedially with corresponding dorsomedial and ventrolateral splints from the maxilla; palate flat posteriorly but slightly excavated anteriorly, bearing scattered palatine foramina, of which the anterior one on each side is the largest; canine crown slightly recurved, covered by slightly irregular

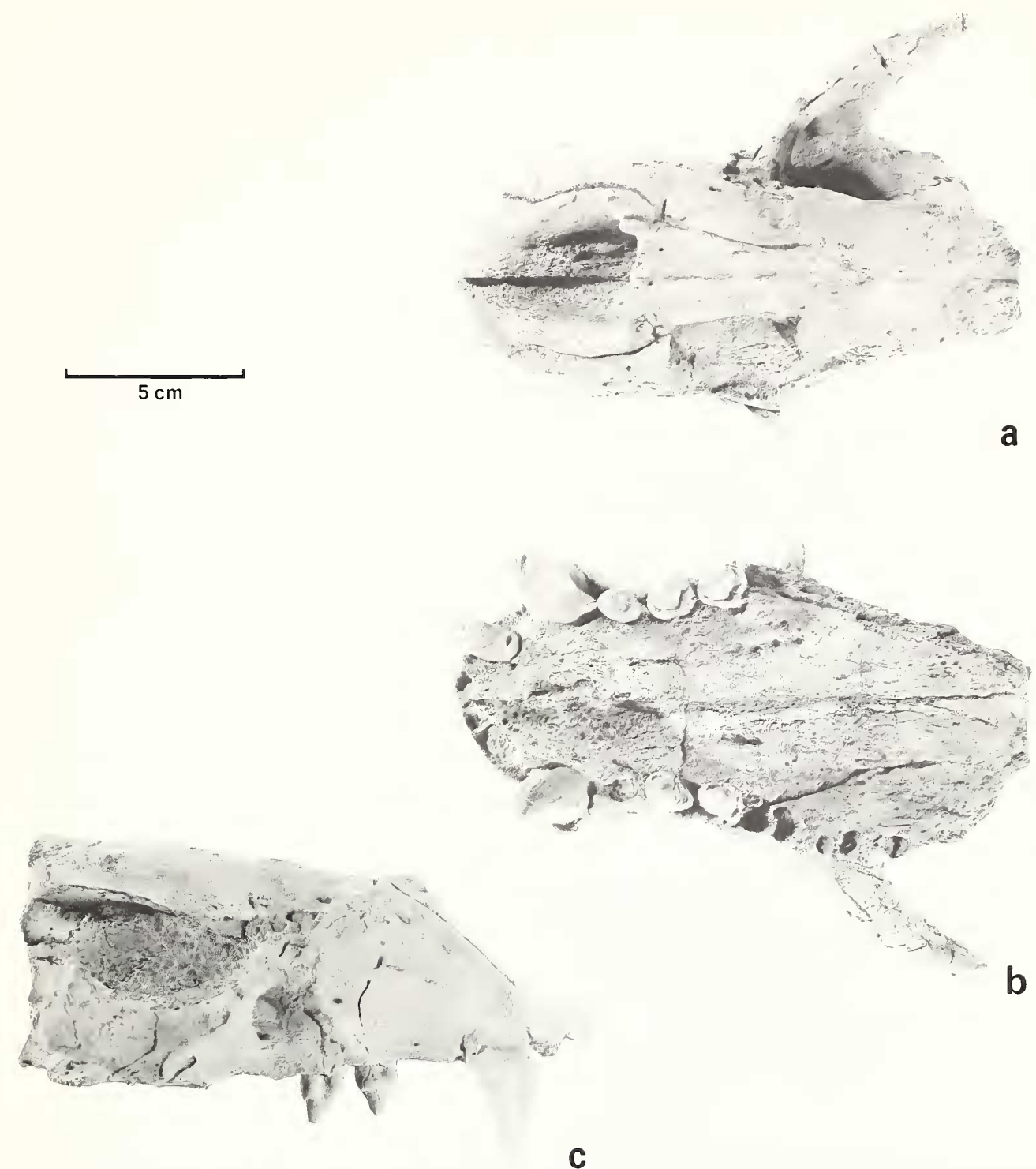


Figure 1. *Desmatophoca oregonensis* Condon, 1906, referred specimen, rostrum, LACM 123285, LACM locality 4851; **a**, dorsal view; **b**, left lateral view; **c**, ventral view.

enamel surface, and bearing a vertical crista posteriorly and a less prominent one medially; and cheek teeth with prominent central cusps and lingual cingulae with small cuspules.

The P¹ has a single, cylindrical root, and on LACM 123285,

its crown has both anterior and posterior cristae. The cingulum is most prominent on the posteromedial side of the crown and extends slightly around the posterolateral side of the crown. The root of P² is clearly bifid on the holotype,

but on LACM 123285 it is bilobed with a deep vertical sulcus on the lateral side. On both specimens, the P³ has two distinctly separate roots, of which the posterior one is bilobed. The tooth is present on both sides of LACM 123285, and its central cusp is high, broad, triangular, and slightly recurved posteromedially. The cingulum is prominent, extends around the medial and posterior sides of the crown, and bears, variably, eight to nine cuspules, of which the most prominent is at the posterior side of the tooth in line with the posterior crista on the crown. On both specimens, the P⁴ has two separate roots, of which the posterior one is larger and transversely bilobed as on the P³. The roots of M¹ on both specimens have patterns similar to those of P³⁻⁴, except that they are smaller and the bilobed posterior root is oriented obliquely.

The referred specimen shows that the species has an M² with a single root, round in cross section, and that the pterygoid process of the maxilla, at the posterolateral corner of the palate, is extensive and thin beneath the orbit. These features of the referred specimen have been incorporated into a modified restoration of the ventral view of the skull of the species (Fig. 9a). The lateral borders of the external narial opening (comprised of the premaxillae) are more rounded on the referred specimen than on the holotype. The zygomatic arch of the referred specimen is not complete enough to provide any additional information on the structure of the squamosal-jugal articulation, which, as shown by a plaster impression on the holotype, was slightly expanded dorso-ventrally.

Desmatophoca brachycephala, new species

Figures 2-8, 9b

DIAGNOSIS OF SPECIES. A species of *Desmatophoca* differing from *D. oregonensis* by having cranium with shorter and wider rostrum, which is more expanded laterally around larger canines; ventral part of external narial opening wider; interorbital region wider, especially in anterior part; zygomatic arch more slender; optic foramina located more posteroventrally within orbits; palate wider, especially in posterior part and having larger pterygoid process beneath orbit; M¹ with only one small, bilobed root rather than two separate roots; M² absent; external acoustic meatus wider and directed more laterally; mastoid process larger and extended more posterodorsally; paroccipital process directed more laterally, instead of posteriorly; posterior lacerate foramen larger and more circular in outline.

HOLOTYPE. LACM 120199, incomplete cranium with crowns of left I¹⁻³, parts of both canines, lacking other teeth and parts of the rostrum, and the right dorsolateral part of the braincase, collected by J.L. Goedert and G.H. Goedert in 1979.

TYPE LOCALITY. LACM 4584 (= LACM Invertebrate Paleontology [LACMIP] locality 5864), east of Knappton, Pacific County, Washington.

FORMATION AND AGE. The type locality of *Desmatophoca brachycephala* near Knappton is in the lower part of a marine rock unit which has been referred to the Astoria

Formation and is Early Miocene, but not earliest Miocene, in age, is correlative with the Pillarian Molluscan Stage, the *Vertipecten fucanus* Molluscan Zone, indirectly correlated with the Saucesian Foraminiferal Stage, and with either the late part of the Arikarean or the early part of the Hemingfordian North American land mammal ages, and therefore is probably between approximately 20 and 23 million years old. This horizon is stratigraphically above the Eocene to earliest Miocene age, marine, Lincoln Creek Formation which crops out down dip and to the west along the Columbia River shoreline. The bases for these determinations are as follows.

The type section of the Astoria Formation is at Astoria, Oregon, directly across the Columbia River south of Knappton, Washington. In her study of the mollusks from the upper part of the Lincoln Creek Formation near Knappton, Moore (1984:1) commented on the age of the Astoria Formation, which directly overlies the Lincoln Creek in this sequence of strata (see also Wells, 1979). Moore also explained that as fossils weather out of exposures of these two formations in the bluffs along the Columbia River, they retain their approximate stratigraphic positions on the beach. This phenomenon is clearly demonstrated by the fact that, over a period of several months, and from a fairly small area, J. and G. Goedert were able to assemble the holotype skull of *D. brachycephala*, as well as other fossils, from broken and extremely weathered parts of concretions.

The type locality of *D. brachycephala* (= LACMIP locality 5864) is approximately one-half km southeast along the north shore of the Columbia River from LACMIP locality 5863, which is shown on the map in Moore's publication (1984:fig. 2). Owing to the dip of the rocks here, the two localities are nearly along strike from one another, and if there is any difference in their stratigraphic positions, the type locality of *D. brachycephala* is possibly only slightly higher in the section than LACMIP locality 5863. These localities are low in the Astoria Formation, have produced fossil mollusks and, based primarily on the occurrence of the bivalve *Acila* (*Acila*) *gettysburgensis*, are assigned to the Pillarian Molluscan Stage (Moore, 1984:1, figs. 2, 3; written communication, 13 August 1986). The mollusk, *Vertipecten fucanus*, which characterizes the Pillarian Stage (Addicott, 1976), has not yet been found at the type locality of *D. brachycephala*, however. The boundary between the Pillarian Stage and the younger Newportian Stage in the Astoria Formation near Knappton, although not yet located biostratigraphically, is presumably north of these localities, and higher stratigraphically within the formation. Much of the type section of the Astoria Formation on the south side of the Columbia River is also referable to the Pillarian Stage (Addicott, 1976:101).

There are some minor conflicts regarding the epochal age designation of these rocks. Following Addicott (1976) and Moore (1984), the Pillarian Stage and the localities in the base of the Astoria Formation near Knappton would fall in the later part of the Early Miocene, but following Armentrout (1981) and Moore and Addicott (1987) they would represent the early part of the Early Miocene.

Regardless of this, the entirety of the Pillarian Stage is older

than the Newportian Stage by definition (Addicott, 1976: 102, 104, fig. 4). Therefore, the section of the Astoria Formation near Knappton that yielded *D. brachycephala* is older than the rocks that are referred to the Astoria Formation near Newport on the Oregon coast, and which produced *D. oregonensis* and the mollusks that were used to characterize the Newportian Stage (see also Addicott, 1976:104). The outcrops of the Astoria Formation near Knappton in Washington that yielded *D. brachycephala* and which contain mollusks of the earlier Pillarian Molluscan Stage may, therefore, represent the early part of the Early Miocene, but are younger than the underlying earliest Miocene part of the Lincoln Creek Formation, are indirectly correlated with the Arikareean North American Land Mammal Age, and may, therefore, be between 20 and 23 million years old. This age determination is most in accordance with the correlations that were proposed by Armentrout (1981).

ETYMOLOGY. The species name, *brachycephala*, is derived from Greek; *brachys*, short, and *kephale*, head; and is in reference to the short snout of this species as compared with *Desmatophoca oregonensis*.

DESCRIPTION AND COMPARISONS. The holotype of *Desmatophoca brachycephala* consists of a nearly complete cranium that was assembled from several pieces of broken fossiliferous rock. These pieces were found within a localized area. From the effects of predepositional erosion and post-depositional breakage, the specimen is lacking all of the cheek teeth, parts of the right and left sides of the palate, parts of the premaxillae, parts of the incisors and canines, the right paroccipital process, and the central and right side of the upper surface of the braincase. It appears to have lain on the seafloor for some time prior to final burial and fossilization, during which time organic and/or inorganic factors caused the erosion of much of the bone surface, principally on the dorsal surface, and the loss of the medial, bony walls of both orbits, the distal ends of the nasal bones, and parts of the nuchal crest. Subsequent tectonic distortion compressed the braincase, the interorbital region, and the tympanic bullae. The holotype of *D. brachycephala* includes structures of the pterygoid hamuli and the zygomatic arches that are not known for *D. oregonensis*. All other parts of the cranium of *D. brachycephala* are directly comparable with corresponding parts on the holotype and the referred specimen (LACM 123285) of *D. oregonensis*.

The holotype of *D. brachycephala* represents an individual in the adult or Group I age class extrapolating from the cranial suture closure method adopted by Sivertsen (1954:10–13) to determine ages of Recent specimens. Of the nine sutures that he found useful for age evaluation, at least seven are closed or mostly closed on the fossil. Because most of the roof of the braincase is missing, only a short section of the interparietal suture is preserved, but it appears to be completely closed. The original degree of closure of the squamosal–parietal suture is difficult to determine. Its course is partly visible on the left side, but distortion has caused the braincase to break along much of that suture. The interfrontal suture is closed, although it appears to be open in the photograph (Fig. 2) because, between the orbits, it is flanked on each side

by an elongate ridge of bone (Fig. 3). The exact suture age of the holotype following Sivertsen's method is therefore not determinable, but it was at least 28. Recent otariids with suture ages of between 19 and 36 are adults (Group I) according to Sivertsen's method.

In addition to the shared diagnostic characters listed for the subfamily (and for the genus), *D. brachycephala* and *D. oregonensis* are demonstrably congeneric because they share the following cranial characters: narrow interorbital region lacking supraorbital processes; interfrontal suture between the orbits flanked by low, elongate ridges; low-vaulted braincase; wide squamosal fossa between the braincase and the zygomatic arch; laterally flaring mastoid process; anterior aperture of the infraorbital foramen slightly overhung by the anterior edge of the orbit; rostrum wider at the canines than at P³; palate relatively flat and expanded posterolaterally ventral to the orbit; more than one posterior palatine foramen on each side, rather than only a single one connected to an elongate and well-developed palatine sulcus; glenoid fossa with a large anteroventrally projecting postglenoid process and small, ventrally directed preglenoid process at the lateral edge only; tympanic bulla relatively flat, with tuberosities limited to the anteromedial part; broad concavity between the middle part of the tympanic bulla and the postglenoid process bearing small postglenoid foramen near the postglenoid process; thin but wide shelf of squamosal bone projecting laterally from the braincase dorsal to the external acoustic meatus; external acoustic meatus entering the bulla in a posteromedial direction; mastoid process approximately cubic in shape, but excavated posteriorly and with a rugose surface facing ventrolaterally; paroccipital process projecting posterolaterally but slightly deflected medially at its termination, excavated ventrally and with a thin anterolateral edge; basioccipital expanded posteriorly, with raised muscular tubercles adjacent to the tympanic bullae, and with a narrow median pharyngeal tubercle which is flanked by relatively deep, hemispherical fossae; hypoglossal foramen small and close to the posteromedial side of the posterior lacerate foramen and with its aperture facing antero-ventrolaterally; occipital condyles projecting prominently from occipital shield with very convex articular surfaces and separated ventrally by a deep intercondylar notch; and foramen magnum wide and low with a thick dorsal margin.

Most of the cranial morphology of *D. oregonensis* has now been documented but, because the descriptions are varied and widely scattered in the literature, a relatively detailed account of the cranial morphology of *D. brachycephala* is warranted here. As in *D. oregonensis*, the rostrum expands gradually anteriorly from its narrowest point in the cheek region around P³, immediately anterior to the infraorbital foramina. The rostrum of *D. brachycephala* is relatively shorter than that of *D. oregonensis*, considering that the crania of the two species have approximately the same zygomatic widths. The external narial opening is widest ventrally and narrower at its apex, the reverse of the condition in *D. oregonensis*. That part of the premaxilla forming the lower lateral border of the narial opening is wide and rounded, as on the referred specimen of *D. oregonensis* (LACM 123285,

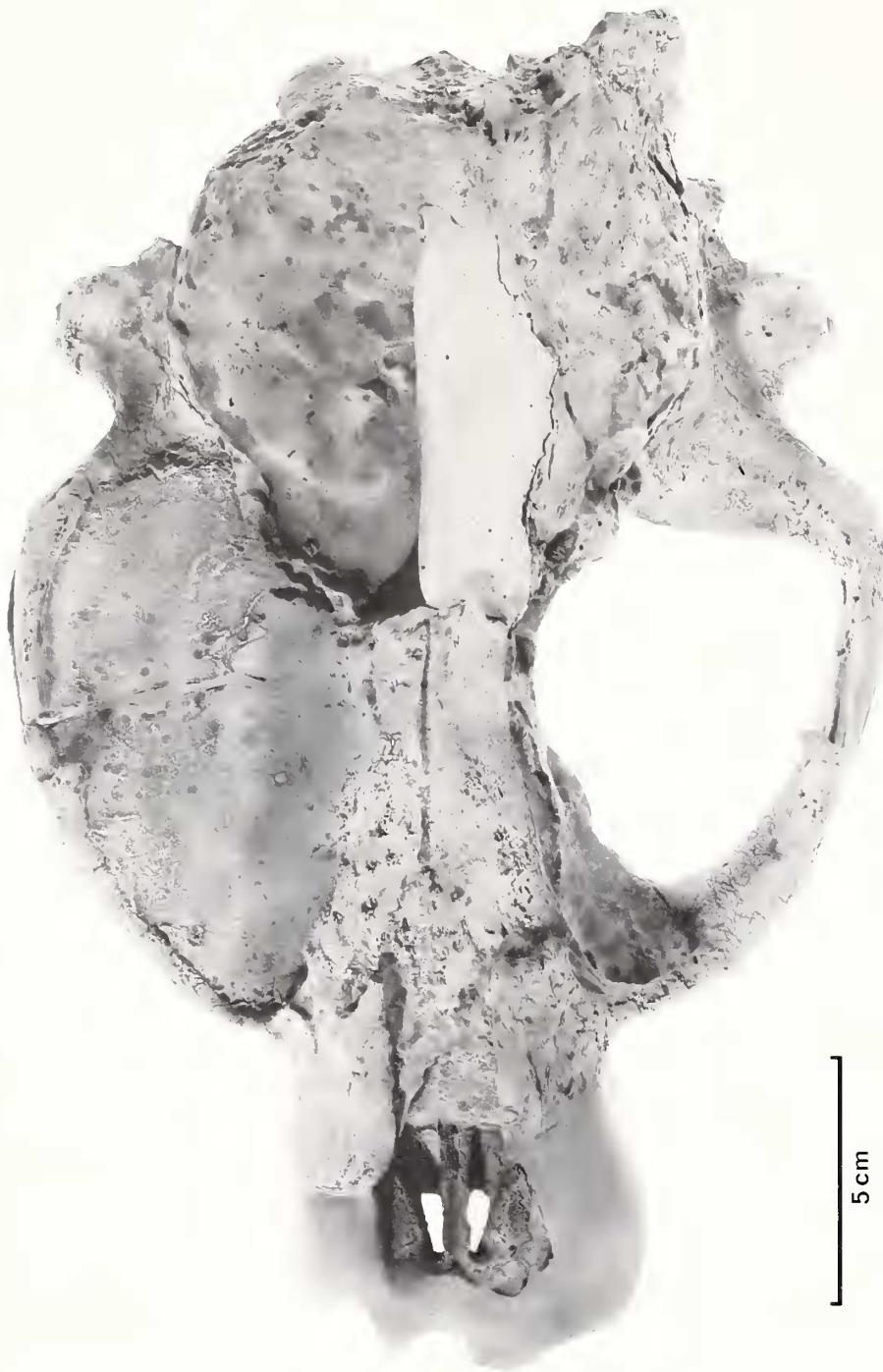


Figure 2. *Desmatophoca brachycephala*, new species, holotype, skull, LACM 120199, LACM locality 4584, dorsal view.

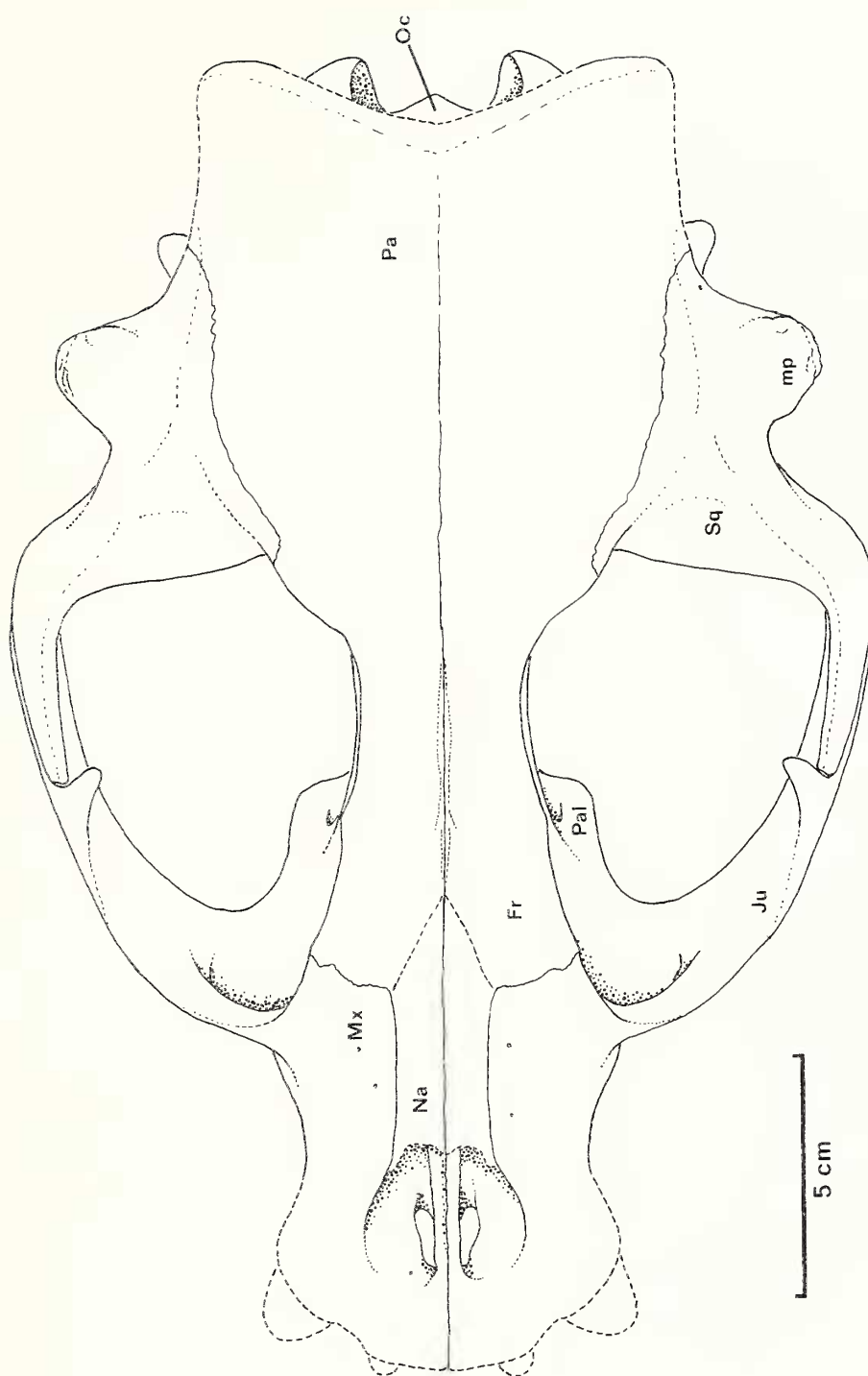


Figure 3. *Desmatophoca brachycephala*, new species, restoration of skull based on holotype, LACM 120199, dorsal view. Abbreviations used in this and following illustrations are explained in the Methods and Materials section.

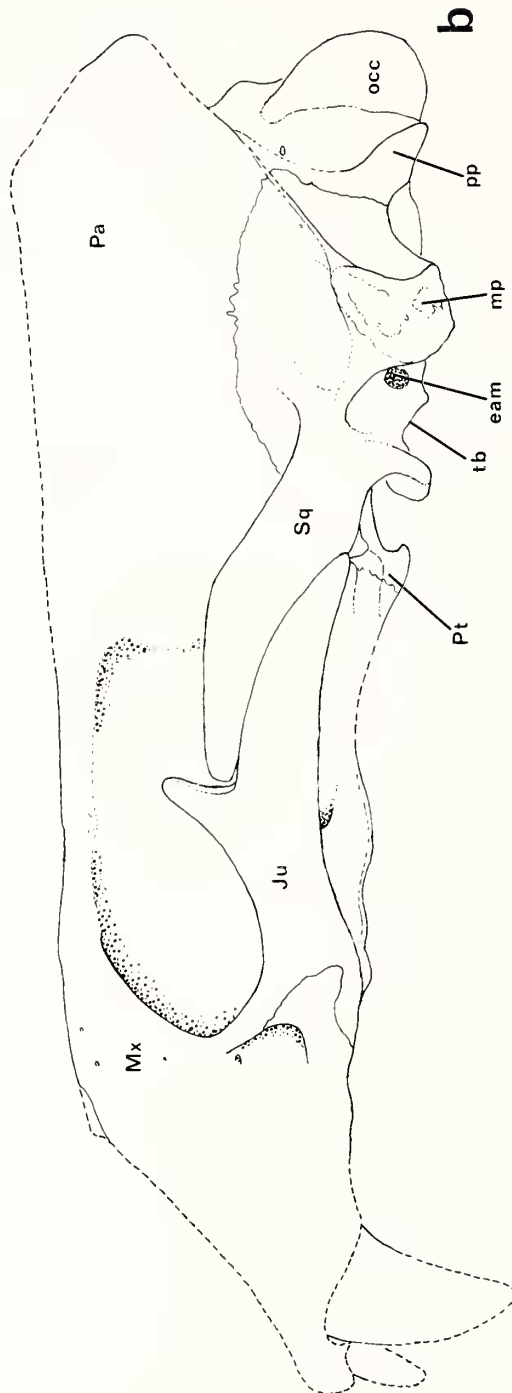
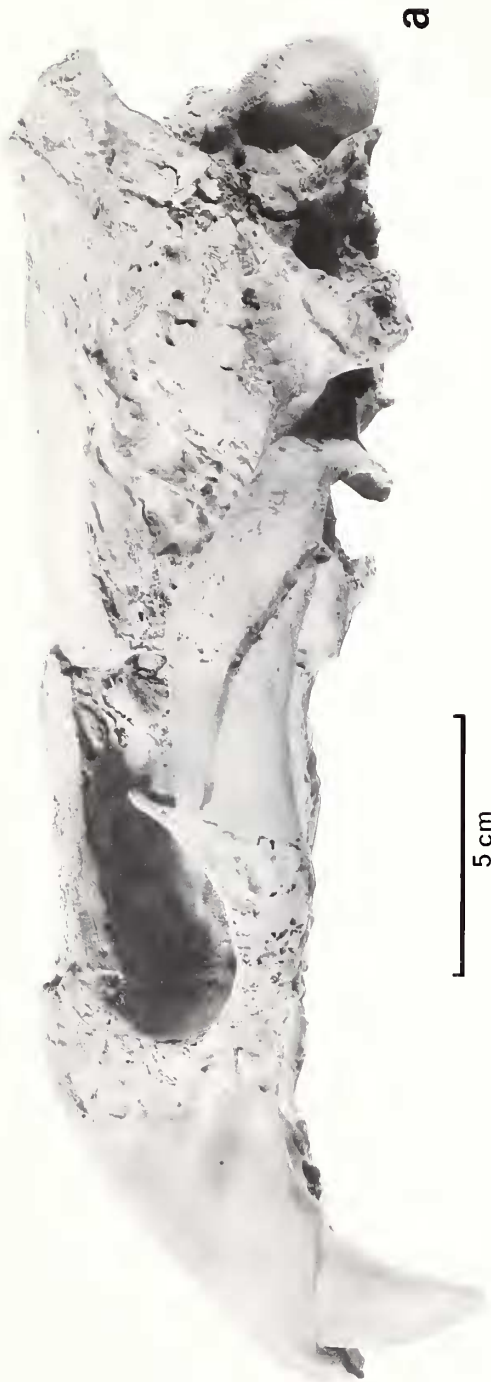


Figure 4. *Desmatophoca brachycephala*, new species, holotype, skull, LACM locality 4584, left lateral view; **a**, photograph of original specimen; **b**, restoration.

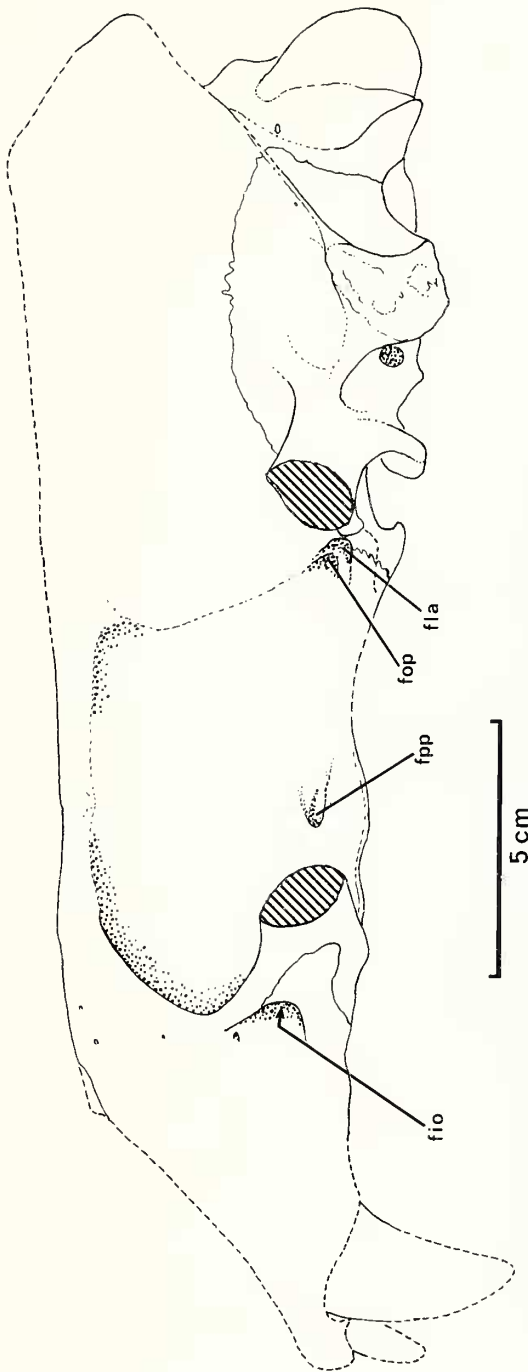


Figure 5. *Desmatophoca brachycephala*, new species, restoration of skull based on holotype, LACM 120199, left lateral view with zygomatic arch omitted to show structures within the orbit.

Fig. 1a), not formed into a narrow crest as on the holotype of *D. oregonensis*. This feature may be variable, therefore, rather than of taxonomic significance. The narial apertures of the incisive foramina are elongate anteroposteriorly and closely appressed, but shorter and more divergent posteriorly than in *D. oregonensis*.

The nasals of *D. brachycephala* are narrower anteriorly than those of *D. oregonensis*. Their combined form is of a tapered wedge extending posteriorly between the frontals, but the sutures at that location are indistinct, and the posterior margins of the nasals cannot be exactly determined. On either side of the nasal bones, the premaxilla-maxilla sutures are obliterated by fusion.

At the anterior margin of the orbit, the dorsal margin of the zygomatic arch flares anteriorly over the anterior opening of the infraorbital foramen and forms a "cup" for the eyeball, much as in the enaliarctines and otariines. This structure is very different from the posteriorly receding dorsal margin of the zygomatic arch in species of *Allodesmus*. The dorsal margin of the zygomatic arch in *D. brachycephala* is narrower and projects farther anteriorly than in *D. oregonensis*.

The interorbital region of *D. brachycephala* is wider and shorter (measuring approximately 20 mm less, anteroposteriorly, between the braincase and the anterior border of the orbit) than in *D. oregonensis*. The sulci on either side of the braincase, which mark the locations of the pseudosylvian sulcus on the brain of *D. oregonensis* (a character also present in *Enaliarctos mealsi* Mitchell and Tedford, 1973), are much shallower and less distinct in *D. brachycephala*. There are also small fossae on either side of the midline on the anterior dorsal part of the braincase in *D. oregonensis*. These are probably homologues of the parasagittal fossae (Mitchell and Tedford, 1973:225) of *Enaliarctos mealsi*, and their presence or absence cannot be determined in *D. brachycephala* due to breakage. The nuchal crest is broken off in the holotype of *D. oregonensis* and, therefore, not known for that species. That part of the crest which is preserved on the holotype of *D. brachycephala* is thick and projects posteriorly over the occipital shield nearly as far as the posterior surfaces of the occipital condyles (Figs. 2, 4a).

The squamosal fossa is the broad recess in the squamosal between the braincase and the zygomatic arch, dorsal to the glenoid fossa, and which floors the temporal fossa. It appears to be characteristically wide in species of Desmatophocinae compared with most other otariids, and is relatively wider in *D. brachycephala* than it is in *D. oregonensis*. Its anterior part, between the anterolateral corner of the braincase and the zygomatic arch, is nearly flat and creates a bony shelf over the anterior part of the glenoid fossa (Fig. 3). The lateral expansion which affected this part of the cranium of *D. brachycephala* also involved the mastoid process, which therefore has a much more extensive, flat dorsal surface than in *D. oregonensis*.

The complete zygomatic arch has not been previously known for the genus, because the structure is missing on the holotype of *D. oregonensis*. This has been the source of some speculation, particularly because the zygomatic arches of the species in the subfamily Allodesminae are greatly modified.



Figure 6. *Desmatophoca brachycephala*, new species, holotype, skull, LACM 120199, LACM locality 4584, ventral view.

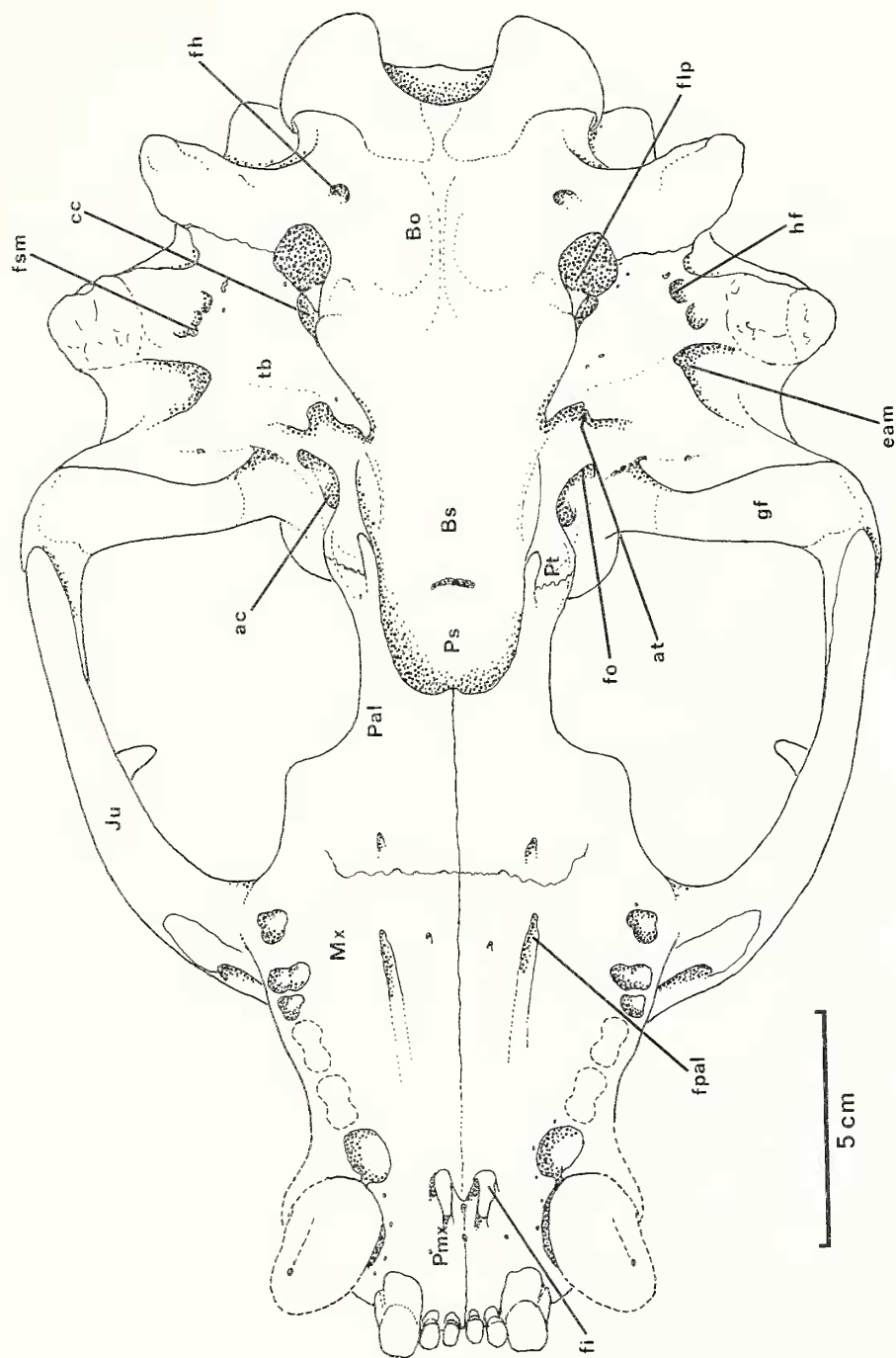


Figure 7. *Desmatophoca brachycephala*, new species, restoration of skull based on holotype, LACM 120199, ventral view.

A matrix impression (see Condon, 1906:3) of the missing part of the right zygomatic arch of the holotype of *D. oregonensis* shows the zygomatic process of the squamosal to be slightly expanded dorsoventrally, but it appears to be basically of the primitive type (Mitchell, 1966:pl. 29d; 1968: 1893; 1975:fig. 2). The right jugal-squamosal junction is completely preserved on the holotype of *D. brachycephala*, and is close to the generalized, primitive carnivore type. The zygomatic process of the squamosal tapers anteriorly to a blunt point which abuts the posterior side of a tapered, dorsally projecting postorbital process of the jugal (Fig. 4b). In the primitive carnivore condition (as in enaliarctines and otariines), the squamosal does not abut the postorbital process of the jugal. Overall, the zygomatic arch of *D. brachycephala* is relatively thick, although not quite as thick as in the preserved comparable parts of the holotype of *D. oregonensis*. The condition in *D. brachycephala* is more primitive than that in *D. oregonensis*, and neither species has the exaggerated vertical expansion of the squamosal and jugal at their junction which is so characteristic of the species of *Allodesminae*.

The palate of *D. brachycephala* is flatter and broader posteriorly, but narrower and more arched anteriorly than that of *D. oregonensis* (Fig. 9). The incisive foramina of *D. brachycephala* are also more divergent posteriorly and recessed more deeply into the palate. The largest posterior palatine foramen on each side opens into an irregularly shaped, elongate palatine sulcus. This pair of sulci differs from those which are characteristic of the species of *Enaliarctos*, which owe their prominence to being sharply defined, parallel, nearly symmetrical, and to not being flanked by other, smaller foramina on the palate. In *D. brachycephala*, as in *D. oregonensis*, each of the large posterior palatine foramina is associated with two or more smaller ones. The expansive pterygoid process of the maxilla beneath the orbit of *D. brachycephala* is even larger than in *D. oregonensis*. It forms a thin infraorbital shelf with a prominent corner. This structure is not as prominent as in the Early Miocene enaliarctine, *Pinnarctidion bishopi* Barnes, 1979, but it is more prominent than in *D. oregonensis* and in the Middle Miocene allodesmine, *Allodesmus packardii* Barnes, 1972.

The crowns of the incisors of *D. brachycephala* are aligned transversely at the front of the palate (Figs. 6, 7). Some distortion may have occurred during fossilization, however, because much of the crown of I¹ is actually farther posterior than the two lateral ones, but the root of this tooth is not present to confirm its exact original alignment. Both I¹ and I² have crowns with their apices worn down to flat surfaces. The crown of I¹ is one-half the diameter of I². More of I³ is preserved than of the two previous teeth. The tooth is very procumbent and its root is oval in cross section. The root is not entirely preserved, but it measures at least 11 mm transversely and 15 mm anteroposteriorly in cross section at the alveolar rim. The crown shows neither cingulae nor cusps as preserved because it has an extensive posterolabial wear facet and its apex is broken off.

Neither canine is complete. All that remains of the right one is the lingual half of the root within the alveolus and,

projecting from the alveolus, is the lingual part of the root at the base of the enamel. The left one is more complete. The lingual side of each canine root has a shallow longitudinal sulcus. The canine of *D. brachycephala* must have been otherwise essentially circular in cross section, and at least 25 mm in diameter at the alveolar rim. I estimate from the remnant of the left canine and the curvature of its alveolar margin that its diameter there was approximately 20 percent greater than in *D. oregonensis*.

There are no cheek teeth preserved on the holotype of *D. brachycephala*. The alveolus for P¹ is located posterolingual to the canine, and is closely appressed to it, so much so that the alveoli of these two teeth are partly contiguous and extremely procumbent (derived conditions). In *D. oregonensis*, this alveolus is more separate from the canine and posterior to it. The lingual side of the alveolus of P¹ has a faint crest, indicating that the root of this tooth had a slight longitudinal, lingual sulcus. The root was otherwise nearly circular in cross section and approximately 10 mm in diameter.

The areas that were occupied by the alveoli for P² and P³ have been broken away on both sides of the skull (Fig. 6), and there is no way to determine the morphologies of these teeth. The space that they occupied on the right side, between the alveoli for P¹ and P⁴, spans only 25 mm anteroposteriorly. This is nearly 15 mm less than the corresponding space on the holotype of *D. oregonensis*, so these two teeth in *D. brachycephala* must have been more crowded together (Fig. 9). Judging from its alveoli, the root morphology of P⁴ in *D. brachycephala* is nearly the same as in *D. oregonensis*. A separate anterior root on this tooth occupied a roughly four-sided alveolus. The primitively separate two posterior roots were fused into a single, transversely bilobed structure (Fig. 7), of which the medial lobe is the homologue of the separate root that is above the protocone in fissipeds and primitive enaliarctine otariids (see Mitchell and Tedford, 1973; Barnes, 1979). In *D. brachycephala*, the P⁴ is located more anteriorly relative to the zygomatic arch than in *D. oregonensis*. The anterior and posterior alveoli of this tooth in *D. brachycephala* are closely appressed, indicating that the P⁴ roots were approaching the stage of fusion (derived character). A diastem of approximately 6 mm, such as is also present in *D. oregonensis*, separates the alveoli of P⁴ and M¹.

The single M¹ alveolus of *D. brachycephala* measures 8 mm anteroposteriorly by 6 mm transversely. It is bilobed, clearly reflecting the root structure of the M¹. The posterior lobe of the root of this tooth was larger than the anterior one. In contrast, as noted previously, the more primitively constructed M¹ alveolus of *D. oregonensis* is double, clearly indicating that the same tooth in that species had two separate roots (Fig. 9). Of these, the anterior root was small and round, and the posterior one was larger and expanded (bilobed) transversely.

An M² was never present in *D. brachycephala*, in contrast to *D. oregonensis*, in which its presence is indicated by an essentially circular alveolus, approximately 7 mm in diameter, on the referred snout (LACM 123285). This loss of M² in *D. brachycephala* is possibly an individually variable character, of course, but if a larger population sample in the future

should confirm that it is diagnostic, then it is a derived feature of *D. brachycephala*. Some individuals of living species of Otariinae experience pathologic or fortuitous loss of the M², but for species in other subfamilies, for example *Allodesmus packardii* and Recent walruses, *Odobenus rosmarus* (Linnaeus, 1758), similar tooth loss is an example of convergence.

The width of the pterygoid of *D. brachycephala* at the level of the pterygoid hamulae is enhanced by a lateral protuberance, which is also present in most otariids except the otariines and *Enaliarctos mealsi*. The pterygoid hamulus is relatively thick, short, and bends ventrolaterally. There is a broad concavity between it and the above-mentioned lateral protuberance.

Most parts of the medial walls of both orbits of the holotype of *D. brachycephala* were broken away and/or decomposed prior to fossilization, and much anatomical information has therefore been lost. No lacrimal foramen is detectable on either the holotype or the referred specimen (LACM 123285) of *D. oregonensis*. Enough of the bone forming the anterior margin of the orbit remains on the holotype skull of *D. brachycephala* to demonstrate the absence of the same foramen in that species as well. In both species there is a small nutrient foramen in the orbit just ventromedial to the orbital aperture of the infraorbital foramen, and, located more posteriorly, is the posterior aperture of the canal leading to the posterior palatine foramina (Fig. 5). Posterodorsal to the latter, on the referred specimen of *D. oregonensis* is a round sphenopalatine foramen, but the holotype of *D. brachycephala* is too damaged in this area to ascertain the location of such a structure.

The area of the orbital aperture of the optic foramen is likewise damaged in *D. brachycephala*, but judging by the curvature of the surrounding bone (Fig. 5), it appears to have been located more posteroventrally (derived character) than it is in *D. oregonensis*. Compared with *D. oregonensis*, the anterolateral corner of the braincase of *D. brachycephala* protrudes farther laterally, as does the pterygoid ventrolateral to the alisphenoid canal, resulting in the creation of a broader, more recessed orbital fissure, which contains the anterior lacerate foramen, the foramen rotundum, and anterior end of the alisphenoid canal. In the posteroventrally recessed position of the orbital fissure as well, *D. brachycephala* is again the more derived of the two species.

Desmatophoca oregonensis and *D. brachycephala* both have the aperture of the foramen ovale recessed in an elongate fossa that is confluent with the posterior end of the alisphenoid canal. This fossa is separated from the medial part of the glenoid fossa by an oblique strut of bone extending to the pterygoid. In both species, the posterior end of the alisphenoid canal is located at a point adjacent to the middle of the glenoid fossa. This is a relatively posterior location (derived) when compared with the anatomy of primitive carnivores, and with that of enaliarctine and otariine pinnipeds, but is not as far posterior as in species of *Allodesmus* (see Barnes, 1972), which have the most derived condition among the otariids.

The glenoid fossa of the squamosal is approximately 45 mm wide and is bordered posteriorly by a prominent, but

relatively thin postglenoid process which projects anteroventrally and is widest medially. In the lateral part of the glenoid fossa, the anterior border is deflected ventrally to create a small preglenoid process. The medial edge of the glenoid fossa, as in *Allodesmus* spp., is marked by a sulcus that curves posteriorly into a small pit, which is probably the anterior end of the canal for the chorda tympani nerve. The lateral ends of the glenoid fossae are canted anterolaterally on the holotype skulls of both species of *Desmatophoca*, but with the present sample, it is not possible to assess whether this is a diagnostic character for the genus or whether it is individually variable as in *Allodesmus kernensis* (see Barnes, 1972). The glenoid fossae on the skulls of both species of *Desmatophoca* are not as rectangular in shape as in species of *Allodesmus*. They enclose nearly 180 degrees of rotational movement of the mandibular condyle by virtue of the prominent postglenoid process and the smaller preglenoid process laterally. The position of the glenoid fossa on the cranium of *D. brachycephala* is farther lateral relative to the tympanic bulla than in *D. oregonensis* (Fig. 9).

The bulla is fused to the postglenoid process over a broad, concave area, at the anterior edge of which is a very small, vestigial postglenoid foramen. Both bullae are damaged on the holotype of *D. brachycephala*, but the right one is the most complete. It is prolonged anteromedially in the form of irregular styliiform processes that extend ventral to the auditory tube (which in life contained, in part, the eustachian tube), the median lacerate foramen, and the anterior end of the carotid canal. A transverse crest on the surface of the bulla extends from this anteromedial part of the bulla to a point ventral to the external acoustic meatus. Anterior to this crest, the bulla surface slopes anterodorsally, but posteriorly it is nearly flat. As in species of *Allodesmus*, and as in *Enaliarctos mealsi* and *D. oregonensis*, the posteromedial corner of the bulla is retracted ventral to the posterior end of the carotid canal, but unlike those species, the bulla is also retracted dorsal to the end of the same canal as well. The effect of this is an enlarged anteromedial part of the posterior lacerate foramen (Fig. 7).

The posterior lacerate foramen is approximately 50 percent larger than in *D. oregonensis* (Fig. 9), and in both species the foramen has an ovoid shape, although it is not as elongate as in *Enaliarctos mealsi* or in species of Otariinae. As is apparently characteristic of the genus *Desmatophoca*, the pit (hyoid fossa) for attachment of the tympanohyoid is not very close to the posterior lacerate foramen (as it is in *Allodesmus* spp.), but instead is positioned on the posterolateral side of the bulla, close to the stylomastoid foramen, and between the bulla and the mastoid process. The tympanohyal pit is separated from the small stylomastoid foramen by only a small crest of bone, but it is separated from the posterior lacerate foramen by a broad, convex surface.

The external acoustic meatus of *D. brachycephala* is wider and directed more laterally than it is in *D. oregonensis*. This is a more primitive morphological state in *D. brachycephala*. The mastoid process is relatively and absolutely larger (derived character), than in *D. oregonensis* and is more rounded in shape (Fig. 9). In contrast to *D. oregonensis*, the process

descends ventrally well below the ventral surface of the tympanic bulla, and projects farther dorsolaterally and is continuous with a prominent but narrow extension of the nuchal crest (Fig. 4). The rugose ventrolateral face of the mastoid process is larger than in *D. oregonensis*.

The paroccipital process differs in both its orientation and shape from that of *D. oregonensis*. This process on both species of *Desmatophoca* resembles those of *Allodesmus* spp. only insofar as this process is large and is separated from the mastoid process by a wide notch. Otherwise, the paroccipital process of *D. brachycephala* (and of *D. oregonensis*) differs from those of species of *Allodesmus* by projecting more posteriorly, not posteroventrally, by being much more flattened dorsoventrally, and by bending slightly medially at the posterior extremity. There is no fossa present on the ventral surface of the skull between the paroccipital process and the tympanic bulla as in species of Enaliarctinae and Otariinae, but the bone surface is instead virtually flat and, in *D. brachycephala*, it is even slightly convex when compared with *D. oregonensis*.

The basioccipital and basisphenoid expand posteriorly in both species of *Desmatophoca*, and the widest part of the basioccipital is between the tympanic bullae (Fig. 9). The holotype skulls of both species are virtually the same width between the bullae. The basioccipital is proportionally wider at this point in *D. brachycephala* than in *D. oregonensis*, however, and the appearance of this is enhanced by the basioccipital being medially constricted posteriorly between the larger posterior lacerate foramina and being more tapered anteriorly toward the basisphenoid. Both species have very prominent fossae for insertion of the rectus capitis longus muscles anterior to the condyles, but in *D. brachycephala* these fossae are wider and shallower and the median pharyngeal tubercle between them is more prominent. Species of allodesmines, enaliarctines, and otariines have less prominent fossae and tubercles, and their extensive development in species of *Desmatophoca* is a derived character.

In both species of *Desmatophoca*, the occipital condyles do not tilt strongly laterally (Fig. 8). They project prominently from the occipital shield and extend ventrally below the ventral surface of the basioccipital. The intercondylar notch is relatively narrow and deep in both species of *Desmatophoca*, especially so in *D. brachycephala*, and somewhat as in *Enaliarctos melesi*. The articular surfaces of the condyles are not bilaterally symmetrical on the holotype of *D. brachycephala*. The one on the left side is abnormal because it does not extend ventromedially as near to the midline as does the one on the right side, nor as do the surfaces on both sides of the holotype of *D. oregonensis*. The foramen magnum of *D. brachycephala* is compressed dorsoventrally (Fig. 8), even more than it is in *D. oregonensis*. There are prominent fossae dorsal to each occipital condyle, and another fossa is centered just below the apex of the occipital shield. Between these, a prominent tubercle extends obliquely dorsolaterally toward the nuchal crest from above each side of the foramen magnum.

RELATIONSHIPS

The subfamily Desmatophocinae can be accommodated within the expanded concept of the family Otariidae that was

used by Mitchell (1968, 1975), Barnes (1972:62; 1979), Mitchell and Tedford (1973), and Hall (1981). There is nothing in the known morphology of either species of *Desmatophoca* that would seem to negate the previously postulated origin of the subfamily from or near a taxon in the Enaliarctinae. Prior characterizations of the desmatophocines as being large, moderately derived, early sea lion-like animals with some retained primitive characters also seem to be correct (Mitchell, 1968, 1975; Barnes, 1972; Repenning and Tedford, 1977; King, 1983:129–130, fig. 3.1). Multiple-rooted posterior cheek teeth, widely separated mastoid and paroccipital processes, relatively primitive and non-mortised (e.g., fissiped-like) zygomatic arches, and small supraorbital processes of the frontal are all primitive characters that the desmatophocines share with the enaliarctines. The relatively elevated position of the optic foramina within the interorbital region of *D. oregonensis*, the loss of M² in *D. brachycephala*, the presence of the anteriorly flared dorsal margin of the zygomatic arch at the front of the orbit, the different shape of the paroccipital process, and other derived characters of both species are some of the ways in which desmatophocines differ from any of the known species in the subfamily Allodesminae. This situation, plus the fact that the unique combination of derived characters of the allodesmines (e.g., exceptionally bulbous-crowned and nearly homodont cheek teeth, lack of vertical carinae on the canines, dorsoventrally expanded (mortised) squamosal–jugal contact, large orbit with its anterior border retracted posteriorly above infraorbital foramen, flatter tympanic bulla, transversely expanded posterior lacerate foramen, and posteroventrally positioned optic foramina within the interorbital region) is not shared with, nor uniquely derivable from the characters of the Desmatophocinae, are part of the argument against either synonymizing the two subfamilies or uniting them in a higher category exclusive of the family Otariidae. In fact, there has been no evidence presented that any members of the other later otariid subfamilies (Otariinae, Imagotariinae, Dusignathinae, Odobeninae) evolved from the Desmatophocinae, and this subfamily appears to have become extinct without leaving any descendants (see Mitchell, 1975; Repenning and Tedford, 1977; Barnes, 1979).

Within the genus *Desmatophoca*, *D. oregonensis* is, in most of its cranial characters, the more primitive of the two known species. Among its most obvious primitive characters are the elongate skull, a smaller posterior lacerate foramen, smaller canine, two separate roots on the M¹, and the retained M². *Desmatophoca brachycephala*, the geochronologically earlier taxon, has only a few characters in which it is more primitive than *D. oregonensis*: a broader interorbital region, a more slender jugal, and a less dorsoventrally expanded squamosal–jugal articulation, for example. It is interesting, though, that in the majority of its cranial characters, *D. brachycephala* is clearly the more derived species of the two because, for example, it has lost the M², has a larger and more cylindrical canine, a single (albeit multilobed) root on the M¹ formed by fusion of previously separate roots, a P¹ which is crowded adjacent to the posteromedial side of the canine, a shorter rostrum, a more anterodorsally flaring anterior margin of the orbit, a larger mastoid process, a smaller and more laterally

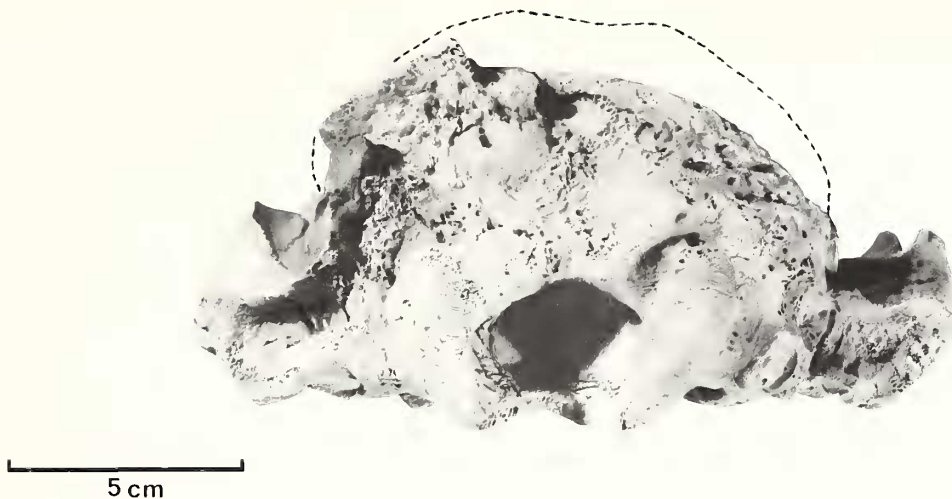


Figure 8. *Desmatophoca brachycephala*, new species, holotype, skull, LACM 120199, LACM locality 4584, posterior view.

directed paroccipital process, the hyoid fossa closer to the stylomastoid foramen and separated from it by only a thin ridge of bone, a broader squamosal fossa, a broader braincase, the mastoid process projecting farther laterally and more deeply excavated posteriorly, and a larger posterior lacerate foramen. The various differences between the two species of *Desmatophoca*, both in geochronological occurrence and in suites of primitive and derived characters, rule out any sort of ancestral-descendant relationship between them. These differences do not preclude the possibility of their sharing a common ancestor, however.

I interpret the above-cited differences as being clearly diagnostic at the species level, and not attributable to individual variation or sexual dimorphism. The holotypes of both species have the kinds of cranial rugosities, crests, and processes that appear as male secondary sex characters in individuals of Recent otariid species, and both holotypes represent adult individuals. Both skulls are nearly the same size, although the holotype of *D. brachycephala*, which is broader and has larger canines, is slightly shorter than that of *D. oregonensis*.

Not only does the discovery of *D. brachycephala* expand the contents and diagnoses of both the genus *Desmatophoca* and the subfamily Desmatophocinae, but it also adds another taxon to the list of examples of cranial convergence between species in the families Otariidae and Phocidae (true seals). Various examples of phocid-otariid convergence have been pointed out by Mitchell (1968:1887–1888, 1892; 1975) and Barnes (1972:63, 64, 66; 1979:30). *Desmatophoca brachycephala* has general cranial proportions similar to those of some phocids, especially the Recent monk seals of the genus *Monachus* Fleming, 1822. The skull of *D. brachycephala* is also broad and dorsoventrally flattened, somewhat as in the allodesmine, *Allodesmus packardii* Barnes, 1972, but differs notably by having more widely flared zygomatic arches and a broader snout.

It is tempting to speculate on the possible life habits of

Desmatophoca brachycephala, but additional specimens would first be necessary. Obvious pinniped characters of the species (e.g., enlarged nares, orbit, braincase, cranial foramina and posterior part of the palate, relatively uninflated bulla, reduced or lost lacrimal bone and lacrimal foramen, near homodonty) indicate that it must have been relatively well adapted to an aquatic existence, but in the absence of information on its middle ear, dentition, mandible, and postcranial skeleton, comments on its diving ability, prey items, mode of feeding, and locomotion would be mostly speculation.

CONCLUSIONS

The extinct subfamily Desmatophocinae is a useful taxonomic grouping within the marine carnivore family Otariidae because it contains morphologically distinctive animals that had a considerable evolutionary history separate from other recognized subfamilies in the family. The Desmatophocinae are apparently not so closely related to the subfamily Allodesminae that the two should be synonymized, an idea that has been supported by some previous authors, including myself. The subfamily Desmatophocinae, now represented by two named species from rocks bordering the eastern North Pacific Ocean, has a known geochronologic range from the Early Miocene to the early Middle Miocene. These are relatively large pinnipeds, apparently relatively rare, which, for their time, and in comparison with contemporaneous and slightly older and smaller species in the primitive subfamily Enaliarctinae, are relatively highly derived. The desmatophocines apparently represent the earliest lineage within the Otariidae to have evolved large size and some derived characters that are convergent with some of those present in the other, later otariid subfamilies. The Desmatophocinae apparently died out without evolving into any later group.

Desmatophoca Condon, 1906, is the type genus of the subfamily. Its type species is *Desmatophoca oregonensis* Con-

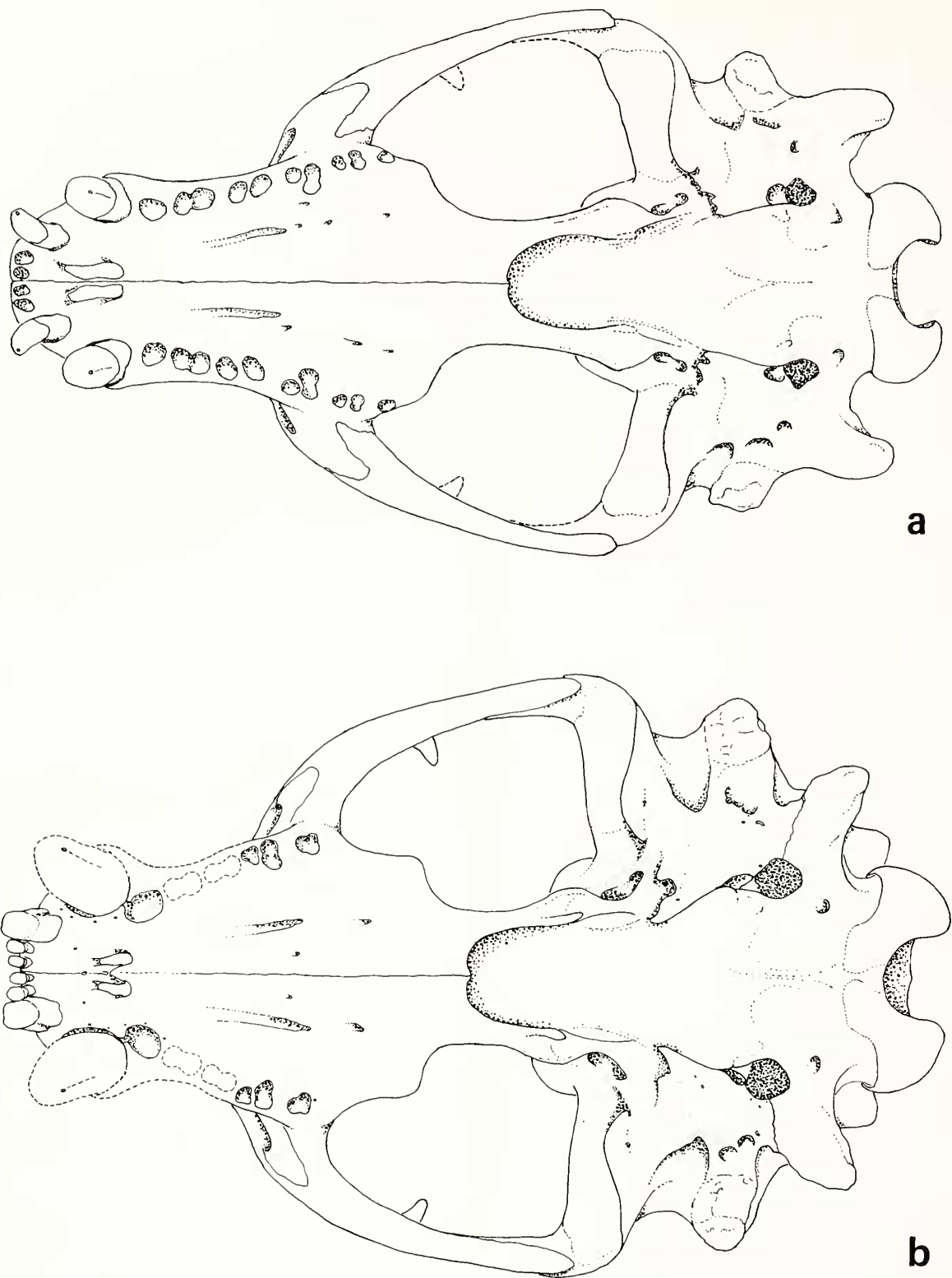


Figure 9. Comparative ventral views of holotype skulls of species of *Desmatophoca*; **a**, *D. oregonensis* Condon, 1906 (modified from Mitchell, 1975:fig. 2, with additional information from referred specimen, LACM 123285); **b**, *D. brachycephala*, new species; reduced to the same cranium length.

don, 1906, known only by specimens from late Early Miocene and/or early Middle Miocene age rocks (circa 15–19 ma) that are referred to the Astoria Formation, and which are exposed near Newport on the Pacific coast of Oregon.

A second species, *Desmatophoca brachycephala*, new species, has been found in slightly older, Early Miocene strata (circa 20–23 ma), that are exposed near Knappton in Washington. The rocks that yielded the holotype and only known specimen of this species have also been referred to the Astoria Formation, but they were deposited in a different sedimentary realm from those on the coast of Oregon, and are correlative with the type section of the formation directly across the Columbia River from Knappton at Astoria, Oregon. Although *D. brachycephala* is the earlier of the two species, judging by most of its characters (broader cranium, shorter rostrum, and other derived dental and cranial features), it is more highly derived than *D. oregonensis*. Neither species is suitable as a morphological or chronological ancestor of the other, but they could share a common ancestor. Like some previously described fossil otariids, some general features of the skull of *D. brachycephala* are convergent with those of true seals in the family Phocidae. It is unfortunate, but probable, that studies of the more numerous specimens of *D. oregonensis*, already in museum collections, will, by inference, provide more information about *D. brachycephala* before additional specimens of this rare pinniped become available.

The discovery of *D. brachycephala* extends the geochronologic range of the genus and of the subfamily farther back in the Early Miocene and indicates that there must have been a considerable, but as yet undocumented, evolutionary history of desmatophocines prior to that time.

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